

Life History of the Funnel-web Spider *Agelena limbata*: Web Site, Growth, and Reproduction

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Abstract The life history of the funnel-web spider *Agelena limbata* was studied in Nagoya located in the central region of Japan. *Agelena limbata* has 1-year life cycle. Instar 1 nymphs emerged from egg sacs in late March to early April and underwent six molts to adults. Males and females matured synchronously and reproduced mid to late August. Most webs were constructed on the evergreen trees which were densely covered with small hard leaves, e.g. *Eurya japonica*, *Ligustrum japonicum*, and *Buxus microphylla*. Fertility was positively correlated with female body size, especially body weight before oviposition. Body size and fertility were compared between two habitats, an open area and a woody field. Body size of adults and fertility were significantly smaller in the open habitat than in the woody habitat. Limited prey availability in the open habitat certainly caused the observed smaller adult size and fertility.

Introduction

Life history parameters are basic components of biology and ecology of organisms. Studies on a life history give important information to comprehend not only many ecological processes but also other aspects of them, e.g. behaviors and physiology.

Spiders are a large group of predators and often abundant in various environments (TURNBULL, 1973), and play an important role as predators in natural and agricultural ecosystems (for review, see RIECHERT and ROCKLEY, 1984; NYFFELER and BENTZ, 1987; TANAKA, 1989 a). Nevertheless there are only a few works that show life history parameters including a survivorship curve or a mortality pattern covering an entire life cycle of a spider species in the field (e.g. EDGAR, 1971 a, b, c; HUMPHREYS, 1975, 1976, 1978; MCQUEEN, 1978, 1983). These studies are all concerned with wandering or burrowing spiders but no study with web-building spiders.

The funnel-web spider *Agelena limbata* (Araneae: Agelenidae) is a common large species (adult body length, 15–16 mm) in Japan (YAGINUMA, 1986). *Agelena limbata* constructs a web on a branch of shrub or tree. This web is not

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adhesive and consists of a flat sheet, funnel retreat, and barrier web. The barrier web is an irregular network of silk strands which serves to knock down flying insects onto the sheet and to prevent prey from escaping. The sheet and funnel are characterized by tight mesh of silk threads and require much energy for construction (TANAKA, 1989b).

I have studied ecology, particularly foraging ecology, of *A. limbata*. To elucidate ecological significance of foraging behaviors, we need to know life history parameters (PYKE et al., 1977). I have so far reported a survivorship curve and mortality factors of *A. limbata* together with some aspects of foraging ecology, i.e. energetic cost of web construction, web relocation rate, and prey capture rate (TANAKA, 1984, 1989b, 1991, in press). This paper describes several aspects of life history of *A. limbata*, i.e. web sites, development, growth, and reproduction.

Materials and Methods

Study area. This study was conducted in two habitats in the campus of Nagoya University, Nagoya located in the central region of Japan. One habitat was a woody field that mainly consisted of deciduous or evergreen, broad-leaved trees. A path ca. 1 m wide runs through the woods. Many *A. limbata* were found around the path but few were found away from the path. The census was carried out within the area 3 m away from the path which covered 1,680 m² (7×240 m). Another habitat was an open area consisting of rows of the box tree *Buxus microphylla*, 0.5–0.8 m high, which were planted on the sides of a road 5.5 m wide. Spiders built webs on *B. microphylla* in this habitat.

Field survey. The populations of *A. limbata* were surveyed 3–6 days a week in the open habitat from late June to September, 1981 and in the woody habitat from late March to September, 1982. I sprayed water on shrubs and trees with a hand sprayer to make spider webs conspicuous and to find them easily. The location of web was identified by attaching a numbered tag to vegetation supporting the web. Web height that was defined as vertical distance from ground to the horizontal sheet web was measured. Spiders which inhabited the webs located above 2 m were not observed as they were difficult to see. But these spiders were only a few.

According to GERTSCH (1970), I define the stages of spiders as follows. Deutovum is an individual which hatched from an egg within an egg sac. The deutovum is inactive and molts to a spiderling in the egg sac. This spiderling that is defined as a first instar nymph emerges and disperses from the egg sac. Spiders after instar 3 were caught and carried to the laboratory for marking. These spiders were anesthetized with carbon dioxide and marks were applied with model-aircraft paint to the tibia of leg-pairs 2, 3, and 4. The marked spiders were returned to their webs around sunset. Preliminary experiments showed that anesthetization and marking appeared to have no detrimental effect on growth or molting of spiders but sometimes caused death to spiders which had just molted. Accordingly spiders were marked more than one day after the molt. When spiders were near to molt, their body color was darkened. Thus, if a newly-molted individual was found on the web where a darkened individual

had been observed at the previous census, I assumed this was the same individual. Instar 1 and 2 spiders were not marked. I assumed an individual which was found on the same web in successive censuses was the same individual in these instars.

After females completed oviposition, I collected the egg sacs and counted the number of eggs.

Determination of spider body size. I measured carapace width of instar 1 to 2 spiders captured near the study field and of instar 3 to adults at the time of marking with an ocular micrometer. Body weight at the beginning of each instar and just before oviposition was estimated by the multiple regression of carapace width (X_1 , mm) and abdominal width (X_2 , mm) at their greatest linear dimension on fresh body weight (Y , mg):

$$Y = a + b_1X_1 + b_2X_2,$$

which was obtained by using data of spiders marked, captured near the study field, or reared in the laboratory. At the beginning of an instar, abdominal width was almost the same as carapace width. Accordingly, initial body weight of an instar was estimated by assuming $X_1 = X_2$ and using carapace width of individuals. Abdominal width of females before oviposition was estimated as follows. Photographs of dorsal view of spiders were taken in the woody habitat 15 and 20 August, 1982, just before oviposition. The ratio X_2/X_1 was determined with the photographs and X_2 was estimated by multiplying this ratio by X_1 which had been already measured.

Results

Web site. Most webs (90.2%) were constructed on evergreen, broad-leaved trees, especially *Eurya japonica*, in the woody habitat (Table 1). Other

Table 1. Vegetation on which *Agelena limbata* construct the webs in the woody habitat.

Vegetation	No. of webs	% of webs
Evergreen trees		
<i>Eurya japonica</i>	357	67.1
<i>Ligustrum japonicum</i>	41	7.7
<i>Quercus glauca</i>	38	7.1
<i>Ilex pedunculosa</i>	14	2.6
Others	30	5.6
Deciduous trees		
<i>Viburnum dilatatum</i>	12	2.3
<i>Rosa multiflora</i>	7	1.3
Others	14	2.6
Others		
Fallen/Cut branches	16	3.0
Others	3	0.5
Total	532	100.0

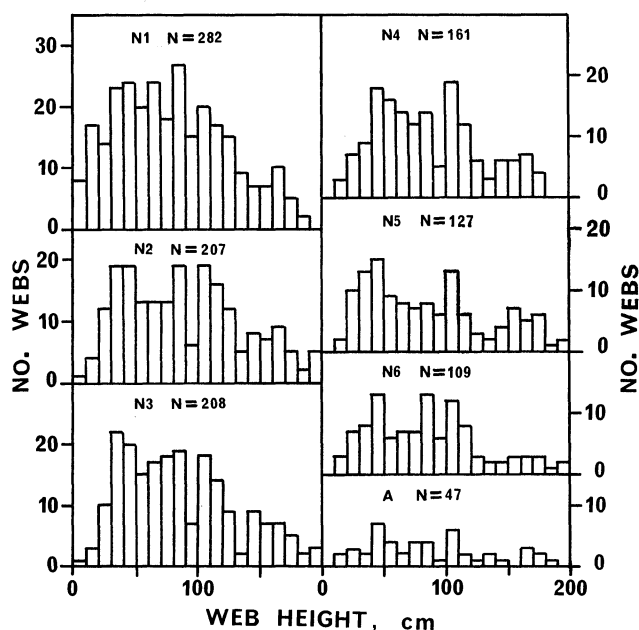


Fig. 1. Frequency distributions of web height of *Agelena limbata* in the woody habitat. N1 to N6 and A indicate instar 1 to 6 nymphs and adult females, respectively.

webs were found on deciduous trees, fallen or cut branches on the ground, litter surface and so on. In the open habitat, many webs were seen on *Buxus microphylla*. These results suggest that *A. limbata* prefers the trees which were densely covered with small hard leaves.

Figure 1 shows the frequency distributions of web height in the woody habitat. The modes of web height were seen between 30 and 110 cm. Distribution of web height was rather different between instar 1 and instar 2 ($P=0.055$, Kolmogorov-Smirnov two-sample test). Many webs were found below 20 cm in instar 1 but a few in the later instars. Later than instar 2, however, distributions of web height did not differ among stages ($P>0.3$).

Durations of instars in the field. Durations of nymphal instars and pre-ovipositional period were observed in the woody habitat (Table 2). Ambient temperatures were also recorded. The durations varied among individuals, the ratios of maximum/minimum duration of each instar being 1.5–2.8. Consequently occurrence of three instars usually overlapped. Males and females matured synchronously. The average molt dates to adult were 24 July for males and 21 July for females. Males stayed on the webs for some days and left the webs probably to search for females. This period varied among individuals, 0 to 13 days (6.3 days on the average).

Body size and growth. Table 3 shows carapace width, initial body weight,

and growth in instars of *A. limbata*. Body weight was estimated by using the regression equations (Table 4) as mentioned earlier. Growth during an instar was defined as difference in initial body weight between two successive instars and daily growth rate as growth/mean duration of the instar (Table 2).

Carapace width and initial body weight of adults were not significantly different between sexes in the woody habitat ($P>0.2$, Mann-Whitney *U*-test).

Table 2. Durations (mean \pm SD) of nymphal instars, preovipositional period, and mean ambient temperatures in the woody habitat.

Stage	N	Duration (days)	Mean temperature ²⁾ (°C)
Instar 1	—	22.0 ¹⁾	14.7
Instar 2	131	13.8 \pm 2.8	16.4
Instar 3	112	16.1 \pm 3.4	18.1
Instar 4	99	17.3 \pm 3.1	20.4
Instar 5	86	21.6 \pm 4.9	21.4
Instar 6	73	26.8 \pm 3.8	21.0
Females	25	31.4 \pm 4.2	23.5

1) Duration from 1 April to the day when 50% of the population molted to instar 2.

2) The mean temperatures were calculated using the values of (maximum temperature + minimum temperature)/2 of each day from the day when 50% of the population molted to the given stage to the day when 50% of the population molted to the following stage.

Table 3. Carapace width (mean \pm SD), initial body weight, and growth of *Agelena limbata*.

Stage	N	Carapace width (mm)	Body wt (mg)	Growth (mg)	Daily growth (mg)
Woody habitat					
Instar 1 ¹⁾	—	1.04 \pm 0.04	2.70	2.82	0.141
Instar 2 ¹⁾	131	1.39 \pm 0.05	5.52	7.68	0.557
Instar 3	112	1.80 \pm 0.15	13.20	15.21	0.945
Instar 4	99	2.28 \pm 0.20	28.41	27.33	1.580
Instar 5	86	2.82 \pm 0.27	55.74	80.34	3.719
Instar 6	73	3.84 \pm 0.39	136.08	125.52	4.684
Males	24	4.79 \pm 0.49	265.38	—	—
Females	44	4.96 \pm 0.42	258.76	266.29	8.481
Before oviposition	25	—	571.28	—	—
Open habitat					
Instar 6	67	3.82 \pm 0.43	133.71	54.48	—
Females	24	4.49 \pm 0.65	188.20	—	—

1) Data from spiders captured near the study field.

Table 4. Multiple regression equations of body weight (Y, mg) to carapace width (X_1 , mm) and abdominal width (X_2 , mm) in *Agelena limbata*.

Stage	N	Regression equation	R ²
Instar 1	35	$Y = -3.53 + 2.52X_1 + 3.34X_2$	0.879***
Instar 2	51	$Y = -17.06 + 8.25X_1 + 7.89X_2$	0.829***
Instar 3	184	$Y = -27.31 + 8.73X_1 + 13.78X_2$	0.947***
Instar 4	131	$Y = -49.00 + 15.09X_1 + 18.80X_2$	0.858***
Instar 5	108	$Y = -103.39 + 28.42X_1 + 27.95X_2$	0.907***
Instar 6	109	$Y = -288.24 + 60.95X_1 + 49.51X_2$	0.950***
Males	21	$Y = -385.80 + 95.36X_1 + 40.50X_2$	0.890***
Females	56	$Y = -480.18 + 44.43X_1 + 104.43X_2$	0.977***

*** $P < 0.001$

Carapace width of instar 6 was similar between the two habitats ($P > 0.2$), suggesting similar growth rate in instar 1 to 5 between habitats. Adult females in the open habitat was, however, significantly smaller than those in the woody habitat and growth during instar 6 in the open habitat was less than a half of that in the woody habitat.

Reproduction. Females in the woody habitat reproduced earlier, 17 to 28 August, than those in the open habitat, 28 August to 21 September. Some females, 5 out of 10 individuals in the woody habitat and 4 out of 23 in the open habitat, produced two egg sacs and the others produced single sacs. Fertilities varied among females, 64–152 (mean \pm SD = 112.4 ± 29.4) in the woody habitat and 12–181 (82.2 ± 43.8) in the open habitat. The mean fertilities significantly differed between habitats ($P < 0.05$, Mann-Whitney *U*-test). Fertility was posi-

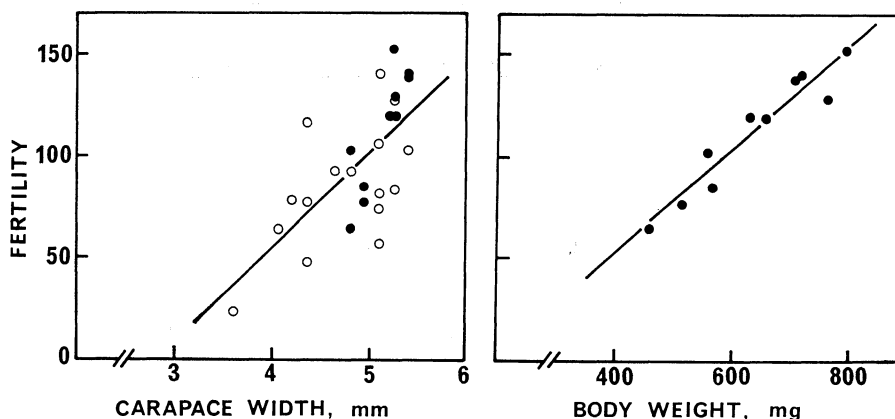


Fig. 2. Relationships between carapace width and fertility (left; $Y = -130 + 46.1X$, $r = 0.679$, $P < 0.001$, $N = 26$) and between estimated body weight and fertility (right; $Y = -50 + 0.255X$, $r = 0.957$, $P < 0.0001$, $N = 10$) in females of *Agelena limbata*. ● Woody habitat, ○ open habitat.

tively correlated with carapace width or estimated body weight of females (Fig. 2). Thus larger females produced more eggs.

Discussion

Life cycle of A. limbata. This paper reveals the life cycle of *A. limbata*. A schema of this life cycle is drawn based on the dates when 50% of the population have entered the following stages in the woody habitat (Fig. 3). *Agelena limbata* has 1-year life cycle. Females produced one or two egg sacs (rarely three egg sacs, MASUMOTO, pers. comm.) in mid to late August. The woody habitat population reproduced earlier than the open habitat population. The open habitat affords poorer prey availability (TANAKA, 1991), which may cause longer time for maturation of an ovary and, therefore, preovipositional period may be prolonged. Females guarded the egg sacs for more than a month. The maternal care reduced mortality caused by predation and abiotic factors (TANAKA, in press).

Eggs hatched to deutova and deutova molted to instar 1 nymphs within an egg sac. Instar 1 nymphs entered diapause (KURIHARA, 1979) and overwintered within the egg sac. These nymphs emerged and dispersed from the egg sac late March to early April and constructed webs. The nymphs underwent six molts to maturity. The number of nymphal instars is constant regardless of food conditions in some spiders including an agelenid (TURNBULL, 1962, 1965) but varies primarily depending on food conditions in other spiders (MIYASHITA, 1968; ROBINSON and ROBINSON, 1978). *Agelena limbata* seems to be the former type of spider. Adults occurred after mid July. Males and females matured synchronously and had the similar body size. Females still remained on webs but males left webs and wandered to search for females to mate.

Web site. Most webs of *A. limbata* were constructed on the trees which were densely covered with small hard leaves, e.g. *Eurya japonica*, *Ligustrum japonicum*, and *Buxus microphylla*. These trees may be profitable for web sites because spiders can easily construct webs on dense leaves and webs constructed on small hard leaves are not easily destroyed by wind. EBERHARD (1971) suggests that web damage by wind affects relocation of web site in the orb weaver *Uloborus*

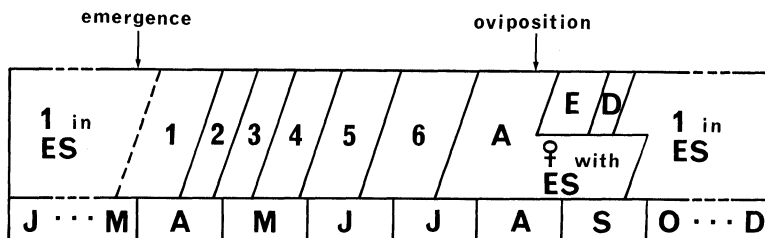


Fig. 3. A schema of life cycle of *Agelena limbata*. E, ES, D, 1 to 6, and A indicate egg, egg sac, deutovum, instar 1 to 6, and adult, respectively.

diversus. Damaged webs capture less prey and spiders should repair or reconstruct the webs. Thus web damage reduces net energy gain for spiders. Especially for *A. limbata*, web damage certainly causes a large energy loss because this spider web is costly to construct (TANAKA, 1989b). Web sites protected from wind, therefore, may be important for *A. limbata*.

Many webs were found below 20 cm in instar 1 but a few in the later instars. This difference in distribution of web height may indicate different mortality between web height. The mortality rate was 36.9% in instar 1 and most of the mortality was accounted for unknown factors (TANAKA, in press). The high mortality at the low web site may be responsible for ground dwelling predators including spiders.

On the other hand, distributions of web height were not different among instar 2 to adults. Webs of the orb weaver *Nephila clavata* were located at higher sites in adults than in nymphs (TOKUMOTO, 1991). No changes in web height of *A. limbata* may be, in part, due to high tenacity on a web site.

Body size and fertility. Body size of adults and fertility were smaller in the open habitat than in the woody habitat. In the open habitat, heat stress suppressed foraging activities of spiders in summer, which resulted in less food consumption, about a half of that in the woody habitat (TANAKA, 1991). The limited prey availability certainly caused smaller body size and fertility in the open habitat population. Heat stress also reduces the prey capture rate of

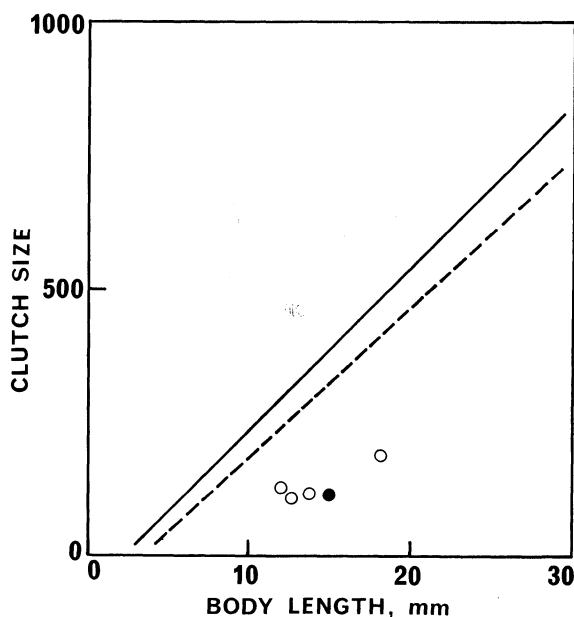


Fig. 4. Relationships of clutch size to body length of adult females. — Regression for web spiders, ---- regression for all spiders, ○ agelenid spiders, ● *Agelena limbata* (modified from ENDERS, 1976).

another funnel-web spider *Agelenopsis aperta* (RIECHERT and TRACY, 1975).

The fertility of *A. limbata* was positively correlated with female body size, especially body weight before oviposition. There are many reports which showed positive correlation between female size and/or food consumption and fertility in the laboratory or field (PETERSEN, 1950; KESSLER, 1971; SUZUKI and KIRITANI, 1974; RIECHERT and TRACY, 1975; WISE, 1975, 1979; MIYASHITA, 1986). Survival rate was also associated with body size in *A. limbata*. Larger individuals survived at a higher rate in some stages (TANAKA, in press). Thus body size of *A. limbata* affected survival rate and female reproductive success which may be related to fitness of individuals.

ENDERS (1976) delineates relationships of clutch size to female body size among spider species (Fig. 4). I added the data of *A. limbata* of the woody habitat on his figure. The data of *A. limbata* far deviates from the regression lines for web spiders or all spiders but is close to those of other agelenid spiders (Fig. 4). The smaller clutch size of agelenids may be related to large egg size (TANAKA, unpublished). Clutch size and egg size may have evolved under influence of many factors, e.g. foraging manners, prey availability, intra- and inter-specific competitions, or phylogenetic constraints. Comparative studies are required to clarify major factors affecting these traits.

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摘 要

名古屋市におけるクサグモの生活史を調査した。クサグモは年1世代であった。1齢幼体は3月下旬から4月上旬に卵囊から出現し、成体になるまでに6回の脱皮を行った。雌雄は同時期に成体になり、産卵は8月中下旬にみられた。ほとんどの網は、ヒサカキ、ネズミモチ、ツゲなど硬く小さい葉が密生した木に造られた。雌当たり産卵数は、雌の体サイズ、特に産卵直前の体重と正の相関があった。クモの体サイズと産卵数を2つの生息地すなわち開けた場所と雑木林の間で比較した。開けた場所の成体のサイズおよび産卵数は、雑木林の個体に比べて有意に小さかった。これは、開けた場所の生息地では餌供給が制限されているためであると考えられた。

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